Osteology and relationships of *Prognathoglossum kalassyi* gen. and sp. nov. (Teleostei, Osteoglossiformes, Pantodontidae) from the marine Cenomanian (Upper Cretaceous) of En Nammoura (Lebanon)

by

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ABSTRACT. - The osteology of *Prognathoglossum kalassyi*, an osteoglossiform teleostean fish from the marine Cenomanian of En Nammoura in Lebanon, is described in details. This fish exhibits an important prognathism. The frontal is broad and short. The temporal fossa is located very laterally on the braincase. There is a small postfrontal behind the frontal. The parietal forms the dorsal border of the temporal fossa. The saccular-lagenar bulla is hypertrophied. This series of specialized characters is shared by the Recent osteoglossoid *Pantodon* and leads to range this Lebanese fossil genus within the family Pantodontidae.

RÉSUMÉ. - Ostéologie et relations de *Prognathoglossum kalassyi* gen. et sp. nov. (Teleostei, Osteoglossiformes, Pantodontidae) du Cénomanien marin (Crétacé supérieur) de En Nammoura (Liban).

L'ostéologie de *Prognathoglossum kalassyi*, un poisson téléostéen ostéoglossiforme du Cénomanien marin d'En Nammoura au Liban, est décrite en détails. Ce poisson montre un important prognathisme des mâchoires. Le frontal est court et large. La fosse temporale occupe une position très latérale sur le crâne. Un petit postfrontal est présent en arrière du frontal. Le pariétal forme le bord dorsal de la fosse temporale. La bulle sacculo-lagénaire est hypertrophiée. Cette série de caractères spécialisés est partagée par l'ostéoglossoïde actuel *Pantodon* et conduit à ranger ce genre fossile libanais dans la famille des Pantodontidae.

Key words. - Teleostei - Osteoglossiformes - Pantodontidae - *Prognathoglossum kalassyi* gen. and sp. nov. - Osteology - Phylogenetic relationships - Marine Cenomanian - En Nammoura - Lebanon.

The marine Upper Cretaceous beds of Lebanon are famous since the Antiquity for their numerous and various fossil fishes. These fishes were cited for the first time in the Armenian translation of bishop Eusebius (c. 265-339) of Caesarea's Chronicles (Gayet *et al.*, 2003: 10). These rich ichthyofaunas have generated a large series of scientific memoirs and papers since almost two centuries (Pictet, 1850; Pictet and Humbert, 1866; Costa, 1857; Davis, 1887; Hay, 1903; Woodward, 1898, 1942; Patterson, 1967; Forey *et al.*, 2003; Gayet *et al.*, 2003; among many others). Three localities, Haqil, Hgula and En Nammoura, are of Cenomanian age, while Sahel Alma is reported to the Santonian.

The aim of our paper is to describe a new osteoglossiform species and genus from the Cenomanian of En Nammoura and to assign its systematic position within the order. That is the first time that a fossil fish belonging to the superorder Osteoglossomorpha is mentioned in the Lebanese Upper Cretaceous ichthyofauna.

The super-order Osteoglossomorpha has a worldwide distribution and is divided into four orders, the Lycopteriformes, the Hiodontiformes, the Osteoglossiformes and the Mormyriformes (= Notopteriformes), of which only the first one is entirely fossil. The three other orders group fossil and Recent members. Some authors consider the Osteoglossiformes and the Mormyriformes as suborders (Osteoglossoidei and Mormyroidei [= Notopteroidei]) that range in an order Osteoglossiformes *sensu lato* (Nelson, 2006: 104). Modern Osteoglossiformes *sensu stricto* often are divided in three families, the Osteoglossidae, Arapaimidae (= Heterotidae) and Pantodontidae (Taverne, 1979: 120-126, 1998: fig. 22; among many others). Some give a subfamilial status to these three families and group them in only one family, the Osteoglossidae *sensu lato* (Nelson, 2006: 104-106). It is to be noted that all the anatomical and most of the genetic analyses give the Pantodontidae as very closely related to the Osteoglossidae. However, Lavoué and Sullivan (2004: figs 2, 3), in a study bearing on more than 4000 characters from five molecular markers, advocate another hypothesis of relationships where the Pantodontidae are no more the sister family of the Osteoglossidae but the plesiomorphic sister lineage of both the Osteoglossiformes and Mormyriformes. A few fossil families and genera *incertae sedis* also are included within the super-order. The oldest osteoglossomorph fishes are Asiatic and date back to the Jurassic-Cretaceous boundary

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(Chang and Miao, 2004: 547). All the Recent osteoglosso-morph fishes inhabit fresh-water environments but the fossil genera are represented by both fresh-water and marine members.

MATERIAL AND METHODS

The specimen belongs to the Luigi Capasso's collection (CLC), which is legally registered by a decree of the Ministero per i Beni e le Attività Culturali under date of October 11th, 1999, following the disposition of the Italian law 1089/39. The Soprintendenza per i Beni Archeologici dell'Abruzzo - Chieti has authorized the authors to study this collection by a letter bearing the date of May 5th, 2011 (reference: MBAC-SBA-ABR PROT 0004537 05/05/2011 Cl. 34.25.01/2.1).

The counterpart of the specimen belongs to the Pierre Abi Saad's collection in Lebanon and is shown in Gayet *et al*. (2012: fig. p. 158) where it is attributed to a possible Lophotiidae.

The material has been studied with a stereomicroscope Leica-Wild M 8. The drawings of the figures were made by the first author (L.T.). Aspersions with ethanol were used to improve the observations.

SYSTEMATIC PALEONTOLOGY

Division **Teleostei** Müller, 1846
Superorder **Osteoglossomorpha** Greenwood *et al*., 1966
Order **Osteoglossiformes** Berg, 1940

Suborder **Osteoglossoidei** Regan, 1909
Family **Pantodontidae** Peters, 1876

Emended diagnosis

Osteoglossiformes with broad and short frontals. Strong prognathism of the lower jaw. Temporal fossa completely located on the lateral face of the braincase. Presence of a postfrontal that forms the anterior border of the temporal fossa. Parietal forming the upper border of the temporal fossa. Hypertrophied saccular-lagenar bulla on the exoccipital and prootic. Ossified orbitosphenoid present. Interopercle absent. Scales not reticulated.

Genus *Prognathoglossum* gen. nov.

Type-species

Prognathoglossum kalassyi gen. and sp. nov. (by monospecificity)

Diagnosis

As for the species (monospecific genus).

Derivatio nominis

From the Greek *pro*, before, in front of, *gnathos*, jaw, and *glôssa*, tongue.

Species *Prognathoglossum kalassyi* gen. and sp. nov.

Holotype and only specimen

Sample CLC S-483, a complete specimen seen by its right side (Fig. 1). Total length: 155 mm.
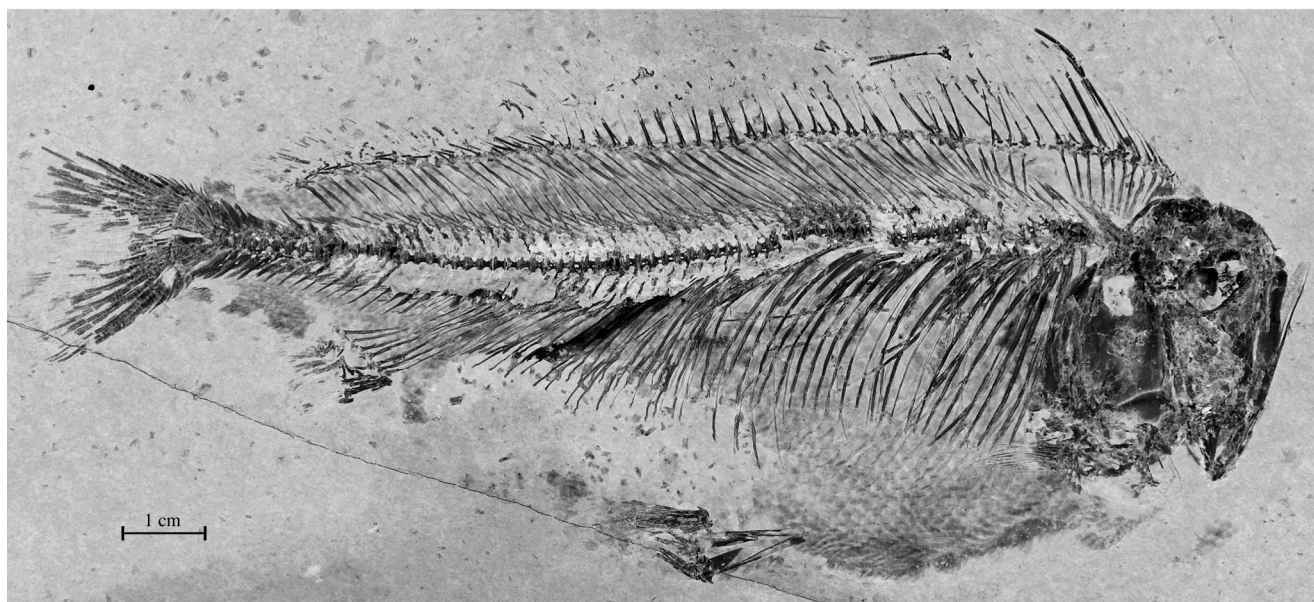

Figure 1. - *Prognathoglossum kalassyi* gen. and sp. nov. Holotype CLC S-483.

Formation and locality

Marine Middle Cenomanian, En Nammoura, Lebanon.

Derivatio nominis

The name of the new species alludes to Lebanese family Kalassy, one of the most active in the fossils collecting in Lebanon. Members of the Kalassy family recovered the specimen described in our paper and furnished it to the co-author (L.C.).

Diagnosis

Thin autogenous dermethmoid bearing one small spine and resting on the massive mesethmoid. Nasals separated from each other. Small supraoccipital without median crest. Plate-like extrascapular covering the temporal fossa. Orbitosphenoid and pleurosphenoids separated from the parasphenoid by a large interocular fenestra. Parasphenoid bearing a few very small denticles. Jaws elongate, prognathous and vertically oriented. Premaxilla with a rank of small hook-shaped teeth. Long toothless maxilla. Angular and articular fused. Elongate retroarticular forming a little part of the articular socket for the quadrate. Antorbital and dermosphenotic well developed. Only four infraorbitals with the third one greatly enlarged and covering the cheek. Preopercle without ventral branch. Large opercle. Reduced subopercle. Dermobasihyal and dermobasibranchial fused in a long lingual plate covered with numerous small hook-shaped teeth and linked to the lower jaw by some ossified ligaments. Cleithrum with equally long dorsal and ventral limbs. Broad hypocoracoid. Pectoral and ventral fins short. Pelvic girdle abdominal. Axial skeleton containing 77 vertebrae (47 abdominal and 30 caudal, including the ural vertebrae). Small centra. Autogenous neural and haemal arches. 41 pairs of ribs. Ossified epineurals and epipleurals present. Long dorsal fin beginning above the supraoccipital, with seven spiny rays, 55 segmented and branched rays and supported by 62 pterygiophores, the first three being very short. Short anal fin with one small spine, nine segmented and branched rays and supported by seven pterygiophores. Preural centrum 1 and ural centra 1 and 2 reduced in length. Preural centrum 1 and ural centrum 1 partly fused. Preural centrum 2 bearing the last complete neural spine. Preural centrum 1 devoid of neural pieces. A short neural spine on ural centrum 1. Only one uroneural. No epural. 6 hypurals. Hypurals 1 and 2 fused together. Hypural 3 broad and fused to the reduced ural centrum 2. Caudal fin forked, with 16 principal rays, eight in each lobe. Small cycloid scales with concentric *circuli*.

Morphometric data

The morphometric data are given as % of the holotype standard length (130 mm) in table I.

Table I. - Dimensions of the holotype given as % standard length (= 130 mm).

Length of the head (opercle included)	20.5%
Depth of the head	25.4%
Maximum depth of the body (between the skull and the pelvic fins)	40.2%
Depth of the body between the pelvic and anal fins	30.4%
Prepelvic length	53.6%
Predorsal length	12.1%
Basal length of the dorsal fin	80.4%
Preanal length	82.1%
Basal length of the anal fin	8.0%
Depth of the caudal peduncle	12.1%

Osteology

The skull

The skull is deeper than long, with very prognathous and vertically oriented jaws that give a general aspect of a bulldog snout (Fig. 2).
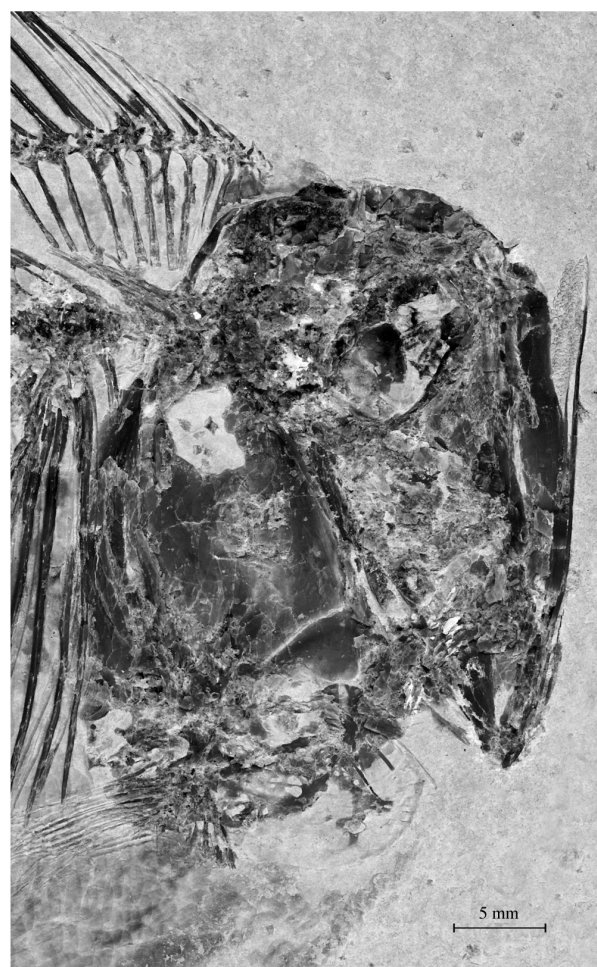

5 mm

Figure 2. - *Prognathoglossum kalassyi* gen. and sp. nov. Skull, pectoral girdle and beginning of dorsal fin of holotype CLC S-483.
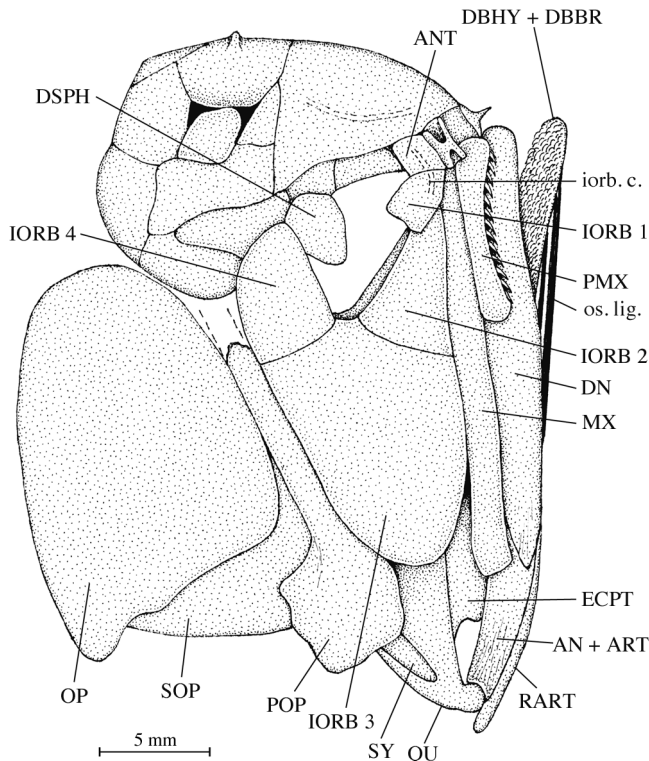
Figure 3. - *Prognathoglossum kalassyi* gen. and sp. nov. Skull of holotype CLC S-483. The neurocranial bones shown on figure 4 are not indicated in the legend.
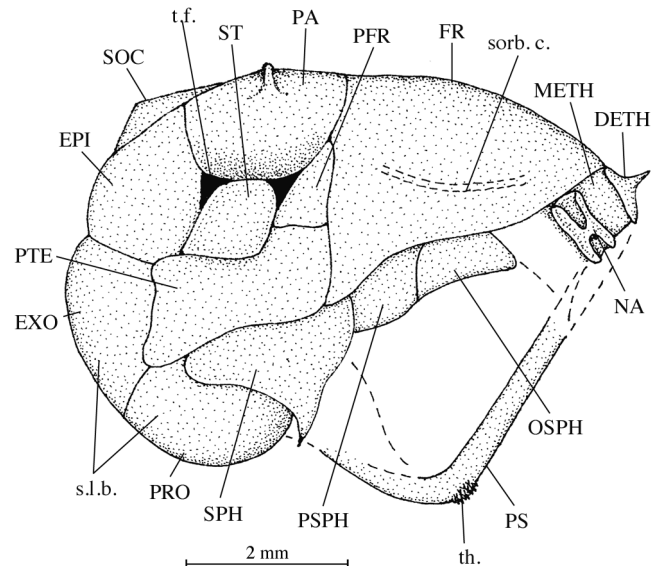

Figure 4. - *Prognathoglossum kalassyi* gen. and sp. nov. Braincase of holotype CLC S-483.

lar bone sutured with the pterotic and bearing a short pointed postorbital process.

The temporal (= posttemporal) fossa is located in a recess of the lateral wall of the skull and not on its rear as usual. The fossa is bordered dorsally by the parietal, anteriorly by the postfrontal, ventrally by the pterotic and posteriorly by the epiotic. A small flat supratemporal (= scalebone, extrascapular) covers the fossa (Fig. 4).

The orbitosphenoid and pleurosphenoids are rather small bones attached just beneath the frontal. They are separated from the parasphenoid by a broad interorbital fenestra. The parasphenoid trabecular portion is rod-like and toothless except in a small posterior region that bears a few very small teeth. The presence of a basipterygoid process is uncertain. The parasphenoid parachordal portion appears as a trace covered by the fourth infraorbital. These trabecular and parachordal parts of the parasphenoid form an almost right angle between them.

The exoccipital and prootic are large and strongly swollen bones, forming an enormous saccular-lagenar bulla. The basioccipital is not visible.

The palatine, metapterygoid and entopterygoid are hidden by the infraorbitals. A small posterior part of the narrow ectopterygoid is visible. The quadrate is triangular in shape, deeper than long, with a big ventral articular condyle and a short quadratic process longing the bone.

The upper and lower jaws are elongated, narrow and extremely prognathous. The premaxilla is rather long and bears a row of small conical teeth strongly inclined backward. Its anterior extremity is slightly deepened but there is no real symphyseal process. The maxilla is toothless. It is an elongate bone reaching anteriorly the symphyseal region

The mesethmoid is a massive bone partly covered by the nasals and by an autogenous thin dermethmoid (= rostral) that bears a unique spine on its centre. The two nasals are separated from each other by the mesethmoid and the dermethmoid. The nasal is long, broad, and carries the most anterior part of the supraorbital sensory canal. This canal remains largely opened. The vomer and the lateral ethmoids are unknown (Fig. 3).

The frontal is short, triangular in shape, posteriorly broad and anteriorly pointed. A part of the supraorbital canal is preserved on the frontal. A small postfrontal lies just behind the frontal and links the parietal and the pterotic. The skull is medioparietal with the parietal well developed and bearing a little crest on its middle part. The surface of the parietal is swollen. Such a swelling could perhaps be due to the presence under the parietal of intracranial vesicles from the swimbladder as in *Papyrocranus afer* (Günther, 1868), an African notopterid fish (Greenwood, 1965: fig. 2; Taverne, 1978: fig. 119-122). The supraoccipital is small and devoid of median crest. The pterotic is a large "L" shaped bone, with a long and broad ventral branch and a short anterior ascending branch longing the frontal and reaching the postfrontal. The epiotic (= epioccipital) also is a large bone. Traces of the lateral and posterior semicircular ear canals are visible on the pterotic and epiotic. The sphenotic is a very big triangu-

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List of abbreviations used in text-figures

AN + ART: angular + articular

ANT: antorbital

AXO: axonost (= proximal element of the pterygiophore)

BAS: baseost (= distal element of the pterygiophore)

BRSP: branchiospines

BRSTG: branchiostegal rays

a., p. CHY: anterior, posterior ceratohyal

CLT: cleithrum

COR: hypocoracoid (= coracoid *sensu stricto*)

DBHY + DBBR: toothed fused dermobasihyal and dermobasibranchial

DETH: dermethoid (= rostral)

DN: dentary

DSPH: dermosphenotic

ECPT: ectopterygoid

EPI: epiotic (= epioccipital)

EPIN: epineural

EPIPL: epipleural

EXO: exoccipital

FR: frontal

HCLT: hypercleithrum (= supracleithrum)

HEM: haemal arch

HEMAP: haemapophysis (= parapophysis)

HEMEP: haemal spine

HY 1 + 2: fused ventral hypurals

HY 3 - 6: hypurals 3 to 6

IORB 1-4: infraorbitals 1 to 4

LEP: fin ray

MES: mesonost (= middle element of the pterygiophore)

MX: maxilla

NA: nasal

NEUR: neural arch

NEUREP: neural spine

NP PU2: neural spine of preural vertebra 2

NP U1: neural spine of ural vertebra 1

OP: opercle

OSPH: orbitosphenoid

PA: parietal

PELV: pelvic bones

PFR: postfrontal

PHY: parhypural

PMX: premaxilla

POP: preopercle

PRO: prootic

PS: parasphenoid

PSPH: pleurosphenoid (= pterosphenoid)

PT: posttemporal

PTE: pterotic

PU 1-5: preural vertebrae 1 to 5

QU: quadrate

RAD 1-14: pterygiophores (= radials)

RI: ribs

SCA: hypercoracoid (= scapula)

SOC: supraoccipital

SOP: subopercle

SPH: sphenotic (= autosphenotic)

SPI: spiny fin rays

ST: supratemporal (= scalebone, extrascapular)

SY: symplectic

U 1, 2: ural vertebrae 1 and 2

UR: uroneural

V: vertebrae

iorb. c.: infraorbital sensory canal

os. lig.: ossified ligaments

sorb. c.: supraorbital sensory canal

s. l. b.: saccular-lagenar bulla

t. f.: temporal fossa

th.: small teeth on the parasphenoid

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just above the premaxilla and bordering the mouth behind the premaxilla. There is no supramaxilla. The mandible is still longer than the upper jaw. The oral border of the dentary is hidden by the premaxilla and maxilla. It is not possible to say if it bears teeth or not. The angular and articular are fused. The retroarticular is long but very narrow. The articular socket for the quadrate is mainly formed by the angular-articular but there is also a little participation of the retroarticular. The mandibular sensory canal is not visible.

The rather small orbit is surrounded by six bones, the antorbital, four infraorbitals and the dermosphenotic. The supraorbital is absent. The antorbital is as long as deep. It is the smallest piece of the orbital series. The first infraorbital is a little larger. The last three infraorbitals are badly cracked but their size and shape are still clearly visible. The second infraorbital is long and posteriorly broadened. These first two infraorbitals form the ventral border of the orbit, while the third and fourth infraorbitals are located behind the orbit. These two posterior infraorbitals are deep and broad, and especially the third bone that becomes considerably enlarged and covers all the cheek. The dermosphenotic offers the same size as the first infraorbital. Traces of the sensory canal are preserved on the antorbital and the first infraorbital.

The preopercle is reduced to a long and narrow dorsal branch. Its ventral part is broken into several small fragments but the general shape of the bone is still visible, showing a posterior enlargement of this region. The preopercular sensory canal is not preserved. The opercle is a large broad bone with the anterior, dorsal and posterior borders slightly rounded and an oblique and slightly concave ventral border. The subopercle bears an anterior dorsal pointed process and is reduced in its posterior part. There is no interopercle. Small fragments of two branchiostegal rays are preserved but partly hidden by the broken ventral part of the preopercle.

The hyoid and branchial skeleton

The lower part of the hyomandibular ventral branch is visible under the fragments of the third infraorbital. The rod-like symplectic is wedged between the quadrate and its quadratic process (Fig. 5).

The dermobasihyal and the dermobasibranchial are fused into a long lingual toothed plate that anteriorly reaches the symphyseal level. The teeth are small, hook-like, sharp and backwardly recurved. A few long and thin ossified ligaments link the plate to the lower jaw.
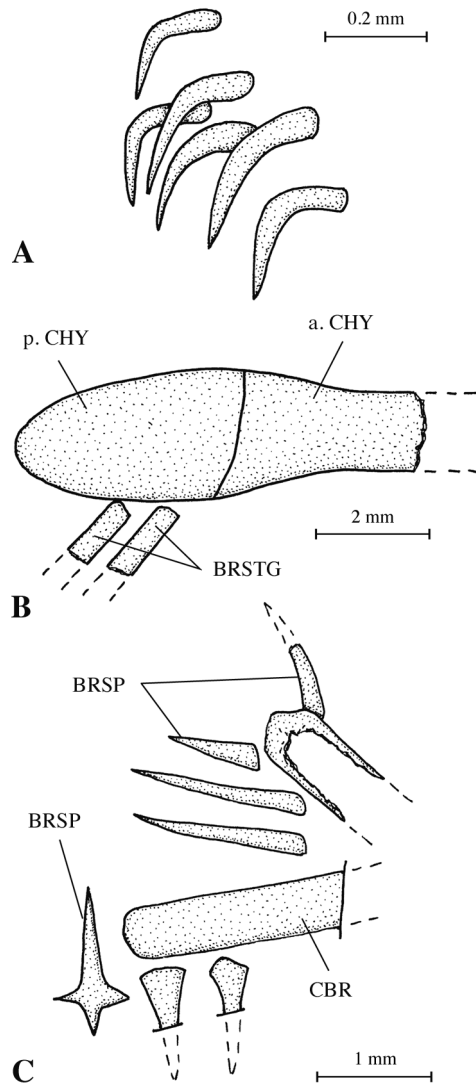
Figure 5. - *Prognathoglossum kalassyi* gen. and sp. nov. **A**: Teeth from the dermobasihyal-dermobasibranchial; **B**: Hyoid bar; **C**: branchiospines with fragments of ceratobranchials of holotype CLC S-483.

Figure 6. - *Prognathoglossum kalassyi* gen. and sp. nov. Pectoral girdle of holotype CLC S-483.

The small hyoid bar is partly covered by remains of the preopercle and of the third infraorbital. The anterior ceratohyal is devoid of beryciform foramen.

A few elongate pointed branchiospines are preserved in the orbit with fragments of ceratobranchials. One of these branchiospines has a triradiate basis.

The girdles

The posttemporal is high with a rod-like upper limb and a triangular lower part. The hypercleithrum (= supracleithrum) is a short flat bone. The cleithrum is large with its dorsal and ventral arms of equal length. There is a small posterior triangular process at the junction of the two arms. No postcleithrum 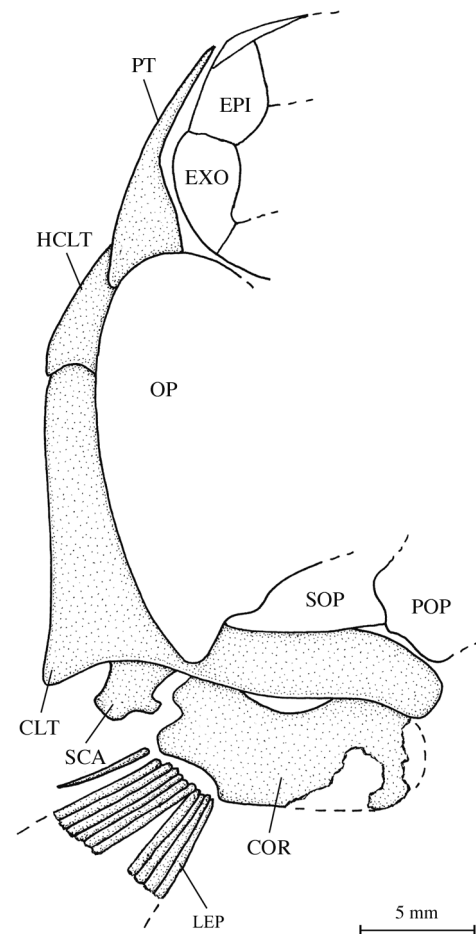is visible. The hypercoracoid (= scapula) is a small bony piece while the hypocoracoid (= coracoid) is a broad bone as long as the ventral limb of the cleithrum. The pectoral fin is short. It begins with a short spine and contains at least about 10 branched and segmented rays (Fig. 6).

The pelvic girdle is abdominal and the origin of the ventral fins lies below thirty-sixth vertebra. The pelvic bones have an elongated triangular shape, with an enlarged posterior extremity. The two bones are separated from each other anteriorly, excepted at their joining tips. They abut one another posteriorly by their broad median processes. At this level, each bone also exhibits a small external pointed process. There is a big comma-like pterygiophore associated with each pelvic bone. The ventral fins are rather short and each of them contains 6 segmented and branched rays (Fig. 7).

The axial skeleton

The vertebral column is completely ossified. There are 77 vertebrae, 47 abdominal and 30 caudal, including the two ural centra. The first five vertebrae are hidden under the supratemporal and the opercle but their neural spines are vis-
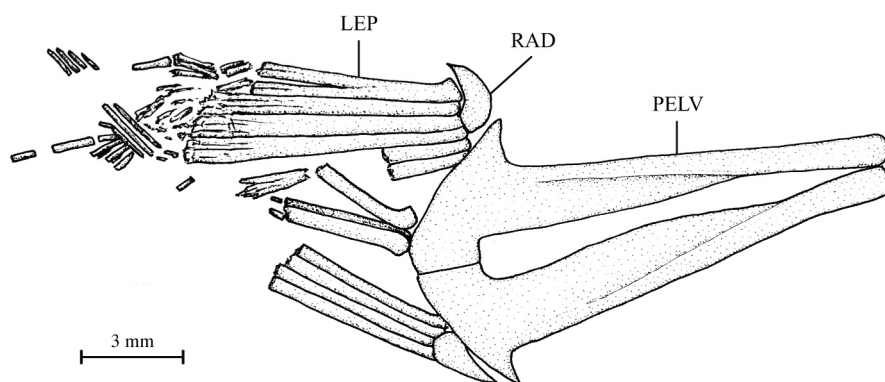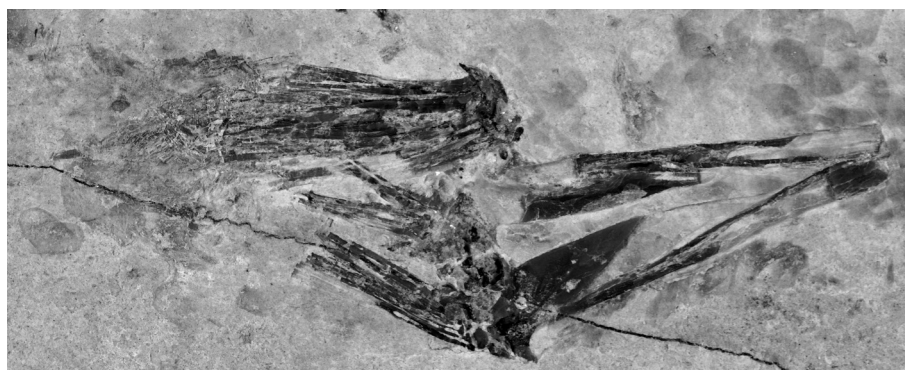
Figure 7. - *Prognathoglossum kalassyi* gen. and sp. nov. Pelvic girdle of holotype CLC S-483.

ible. The centra are small, as high as long and constricted at their middle. The lateral faces of the centra are ornamented generally with one or less frequently with several small pits. The neural and haemal arches are autogenous. The neural spines are long and thin. The haemapophyses (= parapophyses) are short on the first vertebrae but become more and more long on the last abdominal vertebrae. In the caudal region, the neural and the haemal spines have the same length. No supraneural is present. There are 41 pairs of ribs that articulate on the haemapophyses. The first pair corresponds to the seventh vertebra. The ribs are long but do not reach the ventral margin of the trunk. The first ribs are stouter and longer than the last ones. There is a series of long rod-like epineurals extending all along the body. In the abdominal region, the epineurals are inserted on the neural arches, as clearly seen on the 22nd vertebra, but they are autogenous in the caudal region. There is also a series of autogenous epipleurals. They begin at the level of the last ribs and terminate just before the caudal peduncle. The first ones have a bifid posterior extremity. The others are rod-like (Fig. 8).

The dorsal and anal fins

The dorsal fin is very long but not very deep. Its origin is above the supraoccipital and its posterior end is located just before the caudal peduncle. The fin contains seven small spiny rays and 55 segmented and branched rays. The first spiny ray is minute but the six others progressively increase
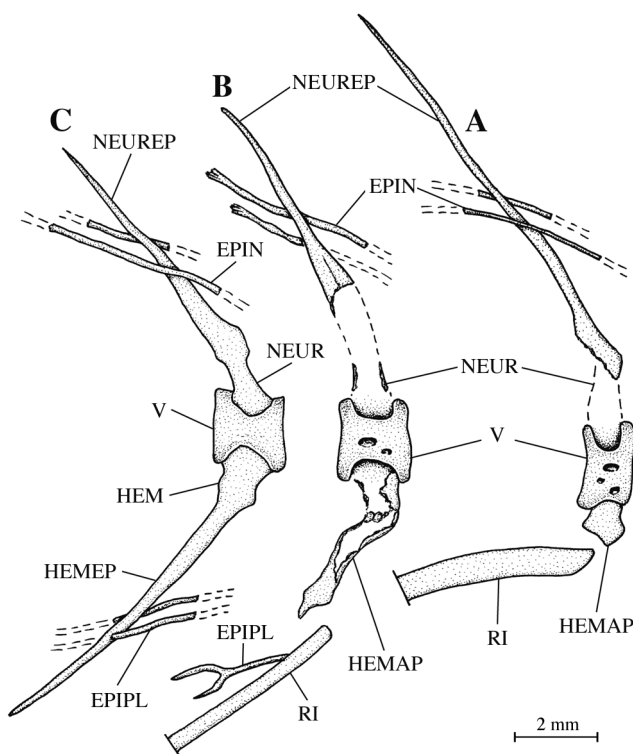

Figure 8. - *Prognathoglossum kalassyi* gen. and sp. nov. **A**: Twenty-second vertebra; **B**: Forty-second vertebra; **C**: Sixteenth vertebra of holotype CLC S-483.
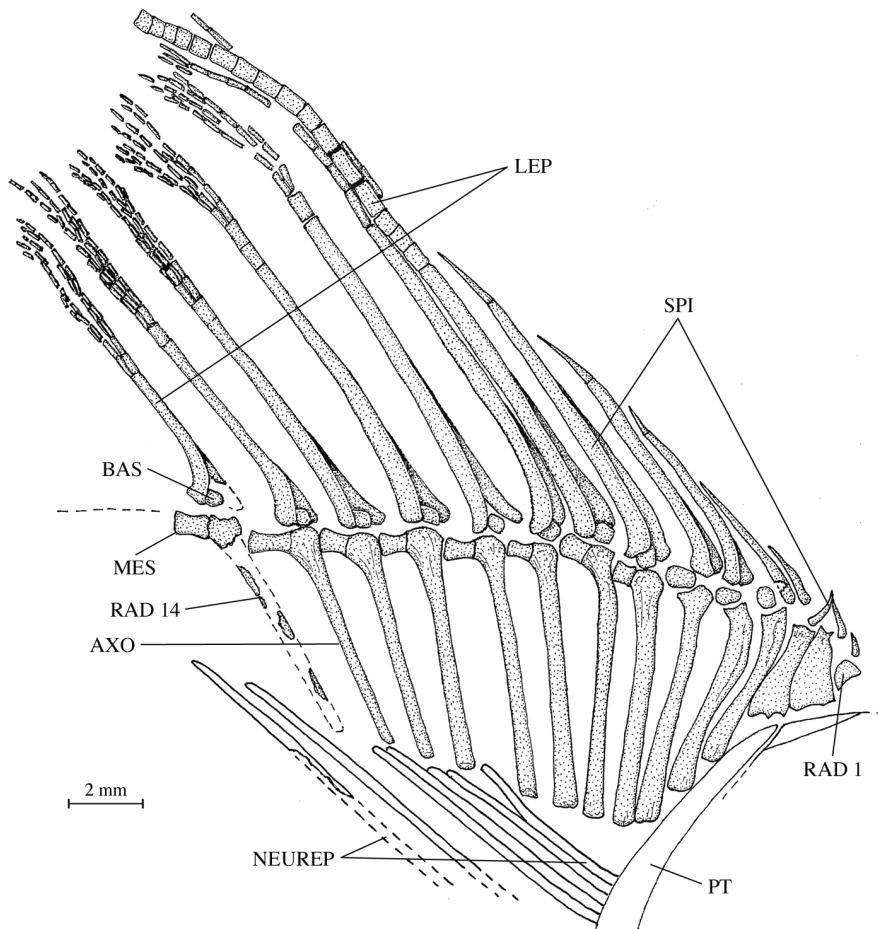
Figure 9. - *Prognathoglossum kalassyi* gen. and sp. nov. Beginning of the dorsal fin of holotype CLC S-483.

1 (PU 1) and ural centrum 1 (U 1) are fused by their upper parts but remain separated ventrally. There is a small ural centrum 2 (U 2) behind U 1. The last neural and haemal arches are autogenous, except the neural arch of U 1 that is fused to its centrum. The last neural and haemal spines are broadened. Preural centrum 2 bears the last complete neural spine (NP PU2). There is no neural element corresponding to PU 1 but U1 has a reduced neural spine. The parhypural is articulated with PU 1. There are six hypurals (HY 1-6). The first two hypurals are fused in a broad ventral plate of which the narrow proximal end articulates with U 1. The third hypural is rather broad and is fused to U 2. The proximal tips of HY 4, 5 and 6 reach the dorsal face of U 2. There is no epural. A unique urone-ural is wedged between NP PU2 and HY 6 (Figs 11, 12).

The caudal fin is forked and contains 16 principal rays, 8 in each lobe. The 2 external principal rays are segmented and pointed. The 14 other principal rays are segmented and branched. There are 10 procurrent rays in the dorsal lobe and 11 in the ventral lobe.

in length. The tip of the last three spiny rays is segmented. The first branched ray is the longest of the series. There are 62 pterygiophores, each bearing a ray. The first one is small. The second and the third are short but broad. The fourth pterygiophore is the first that has a mesonost associated to a long axonost. A small ossified baseost appears from the seventh pterygiophore (Fig. 9).

The short anal fin is preserved partly in bones partly in prints. The fin arises below the 60th vertebra (= preural centrum 16) and begins with a very small spine followed by nine segmented and branched rays. The first ray is the longest. The fin is borne by seven long pterygiophores, each of them being composed of an axonost and a mesonost. An ossified baseost exists at least at the level of the three last pterygiophores. The tip of the first pterygiophore reaches the haemal spine of the 48th vertebra (= preural centrum 28), which is the first caudal (Fig. 10).

The caudal skeleton

The last vertebrae are reduced in length. Preural centrum

The scales

The scales are small, thin, cycloid, more or less circular, and not reticulated. They bear numerous concentric *circuli* on their periphery but no *radii*. The *circuli* are ornamented with very small granulations. The *circuli* disappear in the scale focus (Fig. 13).

Feeding behaviour

Prognathoglossum kalassyi is a piscivorous fish. The digestive tractus of the holotype contains a small teleost of 18 mm in length, swallowed in full.

The long and vertically upwards directed jaws of the Lebanese pantodontid allow a very large opening of the mouth when the lower jaw moves downward. This mechanism, allied with the motions of the opercles, leads to a rapid increase of the volume of the buccal cavity. An important sucking effect is so created that attracts small prey near the mouth. The numerous small hook-like teeth of the jaws and of the tongue then catch these prey that are gulped in one piece, without dilaceration.
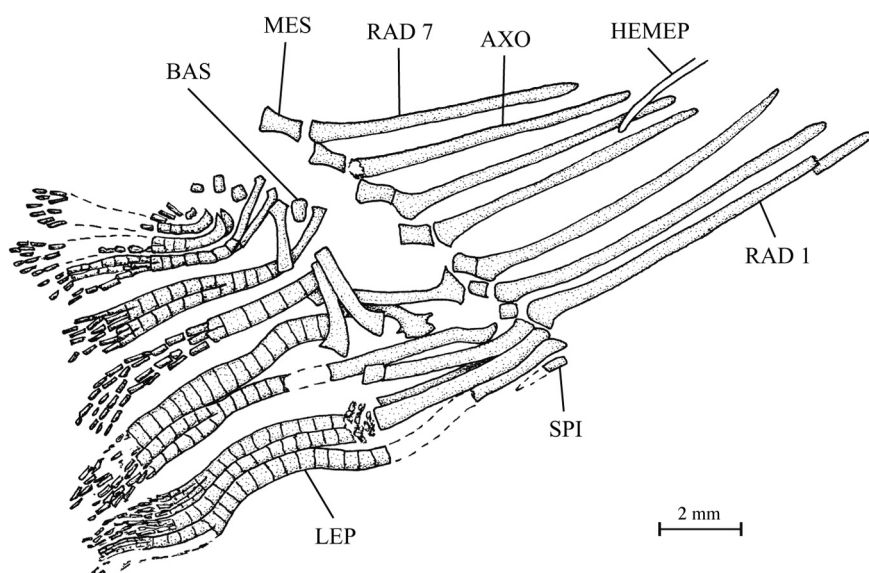
MES   RAD 7   AXO   HEMEP

BAS

RAD 1

SPI

LEP

2 mm

Figure 10. - *Prognathoglossum kalassyi* gen. and sp. nov. Anal fin of holotype CLC S-483.

DISCUSSION

Prognathoglossum within Teleostei

Its maxilla largely bordering the upper jaw, the presence of an orbitosphenoid, its pelvic girdle in abdominal position and the absence of true spines on its dorsal and anal fins indicate that *Prognathoglossum kalassyi* is a rather primitive teleost.

The Cenomanian Lebanese fish also exhibits a peculiar mixing of primitive and specialized characters: (1) the dermethmoid is autogenous, (2) the parasphenoid bears a few small teeth, (3) the antorbital is well developed, (4) there are only two posterior infraorbitals and not three as usual, (5) the third infraorbital is greatly enlarged and covers the cheek, (6) the supraorbital is lost, (7) the posttemporal fossa, covered by a small scalebone, is located on the lateral side of

the braincase and not on its rear, (8) the supramaxilla is lost, (9) the lower jaw is prognathous, (10) the preopercle has no ventral branch, (11) the opercle is large, (12) the subopercle is reduced, (13) the dermobasihyal and the dermobasibranchials are fused into a long toothed plate, (14) the ural centrum 1 bears a neural spine, (15) the epurals are lost, (16) there is only one uroneural, (17) the reduced ural centrum 2 is fused with the third hypural, and (18) the caudal fin has 16 principal rays. Within primitive teleosts, the addition of these eighteen characters is only present in some members of the Osteoglossiformes such as *Osteoglossum* Cuvier, 1829, *Scleropages* Günther, 1864 and *Pantodon* Peters, 1876. We can thus conclude that *P. kalassyi* belongs to this order.

It is to be noted that ossified epipleurals are missing in most osteoglossomorph fishes, except in Notopteridae (Taverne, 1978: fig. 76-80) and in the fossil family Kipalaichthy-
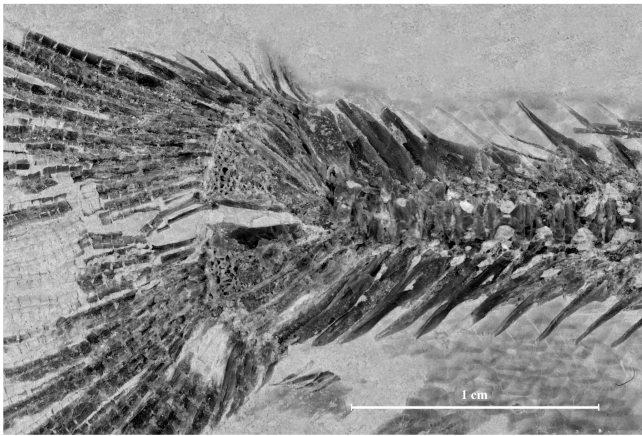
Figure 11. - *Prognathoglossum kalassyi* gen. and sp. nov. Caudal region of holotype CLC S-483.

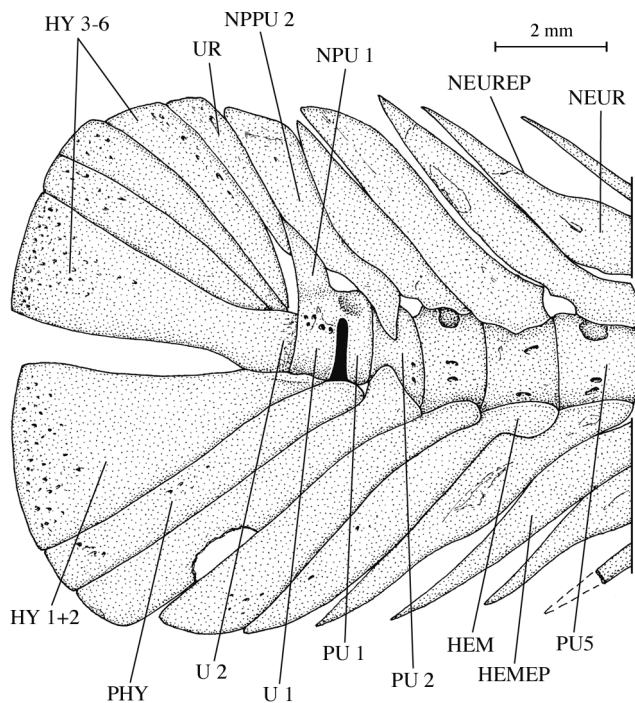Figure 13. - *Prognathoglossum kalassyi* gen. and sp. nov. Scales of holotype CLC S-483

Figure 12. - *Prognathoglossum kalassyi* gen. and sp. nov. Caudal skeleton of holotype CLC S-483.

idae (Taverne, 1976b: fig. 14). *Prognathoglossum*, with its bony epipleurals, is thus another exception within the superorder.

Prognathoglossum within Osteoglossiformes

Taverne (in press: fig. 10, 15-19) has shown that, within Osteoglossiformes, the caudal skeleton exhibits two different lines of evolution. The first one is represented by the Singididae, an African Tertiary family. In these fishes, HY 3 is articulated on the ventral face of a rather long U 2 as in the Chinese most primitive genera of the order. Osteoglossidae, Heterotidae and Pantodontidae form a second evolutionary line in which HY 3 articulates on the rear of the U 2 and no more on its ventral face. In this second lineage, some primitive species have preserved a reduced but still autogenous U 2, while more advanced species have the reduced U 2 fused to HY 3 and sometimes also with the other dorsal hypurals. *Prognathoglossum* clearly belongs to this last osteoglossid subgroup.

The Lebanese fish possesses a highly prognathous lower jaw. Three Recent Osteoglossiformes, *Osteoglossum*, *Scleropages* and *Pantodon*, also present this character (Taverne, 1977: fig. 42, 71, 1978: fig. 30) but not so pronounced as in the fossil genus. The four genera also shared at least two other peculiar characters. Their dermobasihyal and dermobasibranchial are fused in an elongate lingual toothed plate that anteriorly reaches the symphyseal level. Their angular and articular are fused.

Moreover, *Prognathoglossum* and the very specialized genus *Pantodon* shares some other peculiar apomorphies (Taverne, 1978: fig. 31-34, 38, 41): (1) the frontal is broad but very short, (2) the temporal fossa is entirely located on the lateral face of the braincase and has no more contact with its rear face, (3) a postfrontal is present behind the frontal and borders anteriorly the temporal fossa, (4) the parietal forms the dorsal margin of the temporal fossa, (5) the saccular-lagenar bulla is greatly hypertrophied, (6) the interopercle is lost and (7) the scales are not reticulated. However, it is to be noted that, in *Pantodon*, a few scales sometimes exhibit a unique cell in their focus (ibid., 1978: fig. 55). Both *Prognathoglossum* and *Pantodon* also have preserved the orbitosphenoid, a bone already missing in *Osteoglossum* and *Scleropages*.

It is thus clear that *Prognathoglossum* and *Pantodon* are more closely related together than with *Osteoglossum* or *Scleropages*. Both genera could thus be ranged within the family Pantodontidae in spite of the autapomorphies of

Pantodon not present in *Prognathoglossum*, for instance the fused premaxillae, the reduced and tubular antorbital, the lost symplectic, the atrophied supratemporal, the hypertrophied endochondral bones of the pectoral girdle, the very elongated pectoral and ventral fins, the thoracic position of the pelvic girdle, the shortening of the dorsal fin and the swimbladder diverticula entering the enlarged and cavernous haemal apophyses (Nysten, 1962; Kershaw, 1970, 1976; Taverne, 1974, 1978, 1998; among others). Inversely, the Lebanese fossil pantodontid also exhibits autapomorphies absent in *Pantodon*, such as the toothless maxilla, the bony ligaments linking the dermobasihyal and the lower jaw, the hypertrophied sphenotic, the very long dorsal fin beginning above the occipital region, the presence of ossified epipleurals, the partial fusion between PU 1 and U 1 and the loss of the neural elements on PU 1.

Paleozoogeographical implications

Since the Early Cretaceous (Aptian) osteoglossomorph *Laelichthys ancestralis* Silva Santos, 1985 from Brazil is found in brackish deposits, *Prognathoglossum kalassyi* is the oldest marine osteoglossomorph discovered so far. Moreover, the relationships of the Brazilian species with the Osteoglossiformes are still uncertain and need further investigations.

The presence of *Prognathoglossum* in the Eurafrican realm of the Tethys Ocean during the Cenomanian states the problem of its origin.

During the Early Cretaceous, Osteoglossiformes are well represented in a few Asian deposits of freshwater origin, with genera such as *Yungkangichthys* Chang & Chou, 1974 from Japan, *Paralycoptera* Chang & Chou, 1977 from eastern China, *Aokiichthys* Yabumoto, 1994 from Japan and *Xixiaichthys* Zhang, 2005 from central China (Yabumoto, 1994; Zhang, 2005; Xu & Chang, 2009). But all these occurrences are from East Asia, a region very distant from Lebanon. So, an Asiatic origin for *Prognathoglossum* is greatly improbable.

In the Lower Cretaceous continental deposits of Africa only one unique osteoglossiform genus has been reported until now, *Chanopsis* Casier, 1961 from the Democratic Republic of Congo [DRC] (Taverne, 1984; in press). However, a second osteoglossoid also exists in the Lower Cretaceous of the DRC (unpubl. pers. obs., paper in prep.). During the Cenomanian, two other osteoglossiform fishes are known in the same country but in a marine environment, *Paradercetis* Casier, 1965, a fossil genus closely related to the Recent African *Heterotis* Cuvier & Valenciennes, 1846, and *Kipalaichthys* Casier, 1965 (Taverne, 1975, 1976a, 1976b). These two last fishes belong to the Kipala ichthyofauna, a fish community that presents affinities with the Cenomanian marine ichthyofauna of Lebanon (ibid., 1976b: 42-43). An African origin for *Prognathoglossum* is thus the most prob-

able hypothesis, the more that its closer relative is the Recent African genus *Pantodon*.

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